

## VARIATION IN INCUBATION PATTERNS OF RED-WINGED BLACKBIRDS NESTING AT LAGOONS AND PONDS IN EASTERN ONTARIO

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**ABSTRACT.**—We studied incubation patterns and hatchability of Red-winged Blackbirds (*Agelaius phoeniceus*) nesting in two different wetland habitats—beaver ponds and sewage lagoons—in eastern Ontario during 1999–2001. We presumed that, if incubating Red-winged Blackbirds could acquire food more readily at sewage lagoons than at beaver ponds, they should respond by taking fewer and shorter foraging bouts, which would result in longer bouts of attentiveness, shorter incubation periods, and higher hatchability of eggs. Although differences were small, female foraging bouts were shorter and bouts of attentiveness were longer at sewage lagoons than they were at beaver ponds. Incubation constancies were subsequently greater, and, ultimately, incubation periods at sewage lagoons were shorter. Shorter incubation periods at sewage lagoons, however, did not result in increased hatchability. Our results suggest that, in habitats where incubating Red-winged Blackbirds can acquire food more readily, incubation periods may become shorter and incubation constancies may become higher. Received 7 September 2004, accepted 28 April 2005.

Many species of temperate-zone passerines modify incubation patterns in response to variation in nutrient availability (Hebert 2002, Eikenaar et al. 2003), frequency of mate feeding (Nilsson and Smith 1988, Pearse et al. 2004, Radford 2004), body mass (Williams 1991), temperature (Conway and Martin 2000a, Reid et al. 2002), and nest predation (Martin and Ghalambor 1999, Conway and Martin 2000b, Ghalambor and Martin 2002). Eggs of most passerines must be maintained at a temperature of 34–39° C for optimal embryonic development (Drent 1975, Webb 1987, Williams 1996). Ambient temperatures, however, rarely remain within this range, and deviations in egg temperatures can affect incubation period and egg hatchability (Strausberger 1998); therefore, incubation by parents is required to prevent embryos from chilling or overheating.

When ambient temperatures are low, incubation can be energetically demanding for parents, requiring an increase in metabolic rate to a level approaching that experienced during chick-rearing (Williams 1996, Thomson et al. 1998, Visser and Lessells 2001). Hence, energetic demands during incubation may have fitness consequences: adult body condition may deteriorate, or adults may be

unable to provide conditions conducive to embryonic development. Fitness consequences will be especially severe where only the female incubates (gyneparental systems) and where bouts of attentiveness are interspersed with foraging bouts (Williams 1996).

In gyneparental systems, daytime incubation is usually intermittent because females must balance the time spent foraging against the thermal needs of the developing embryos and the energetic demands of rewarming the clutch after a foraging bout. Most reviews of avian incubation suggest that the duration of attentiveness bouts (interval during which the female incubates between two foraging bouts) is dictated by the female's energy needs (Kendeigh 1952, Haftorn 1978, Weathers and Sullivan 1989, but see Conway and Martin 2000b). If the energy needs of the female are an important factor affecting incubation patterns, then nest attentiveness should increase in relation to the rate at which food can be acquired (i.e., food acquisition) during foraging bouts, the incubation period should be shorter, and hatching success should increase (Martin 1987). Thus, species that use more energetically expensive foraging strategies or forage in habitats where food items are less available may have to spend more time foraging or engage in more frequent foraging bouts to meet nutritional requirements.

Although there have been few studies of variation in passerine incubation patterns, presumably because these data are time-consum-

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ing and laborious to collect, results from several of these studies (e.g., Nilsson and Smith 1988, Moreno 1989, Sanz 1996, Pearse et al. 2004) suggest an important relationship between nutrient availability and incubation patterns. For example, studies on Northern Wheatears (*Oenanthe oenanthe*; Moreno 1989), Blue Tits (*Parus caeruleus*; Nilsson and Smith 1988), and Pied Flycatchers (*Ficedula hypoleuca*; Sanz 1996) have revealed that females receiving supplemental food during incubation had significantly shorter incubation periods and/or their clutches experienced greater hatchability (but see Pearse et al. 2004). Moreover, there should be a premium on short incubation periods, which reduce the time that eggs are vulnerable to predators (Clark and Wilson 1981, Conway and Martin 2000a, Martin 2002).

As far as we know, there have been no studies that have evaluated variation in incubation patterns related to foraging habits or food acquisition between habitats. Using a comparative approach, Reid et al. (1999) suggested that the duration of foraging bouts among European Starlings (*Sturnus vulgaris*) was more than four times longer (20 min versus 4.5 min) on Waddensea Island (from Drent et al. 1985) than on Fair Isle, where incubating adults could feed in close proximity to their nest cavities, reducing the time and energy needed to travel to foraging areas. In addition, Reid et al. (1999) suggested that, because the ground on Fair Isle remained permanently damp, it was unlikely that the starling's invertebrate prey would be difficult to obtain during any period of the day. However, because Waddensea Island and Fair Isle differ substantially in latitude, climate, and habitat, comparison of incubation patterns between these islands was not feasible (Reid et al. 1999).

We examined habitat-related variation on gyneparental incubation patterns, incubation periods, and hatchability of eggs by studying Red-winged Blackbirds (*Agelaius phoeniceus*) nesting at numerous sewage lagoons and beaver ponds in eastern Ontario. Extensive data have suggested that food availability is greater at sewage lagoons than in other habitats during the breeding season of many bird species (e.g., Swanson 1977, Piest and Sowls 1985, Hussell and Quinney 1987, Porter 1993, Zimmerling 2002). For example, during laying, in-

cluding a natural cattail marsh (Hussell and Quinney 1987). During the brood-rearing period in eastern Ontario, female Red-winged Blackbirds at sewage lagoons captured a mean of nine insects per foraging bout, whereas females at beaver ponds captured one to two insects per foraging bout (Zimmerling 2002). Therefore, we predicted that females nesting at sewage lagoons would take fewer and shorter foraging bouts than females nesting at beaver ponds. Consequently, we also predicted that incubation periods would be shorter and egg hatchability greater at sewage lagoons.

## METHODS

*Study area.*—From 1999 to 2001, we studied Red-winged Blackbirds nesting at wetlands in eastern Ontario between Cobden (45° 40' N, 77° 10' W) and Vankleek Hill (45° 35' N, 74° 40' W; see Zimmerling 2002). Wetlands in the study area included 19 small (0.3–3 ha) beaver ponds (hereafter, ponds) and 10 municipal sewage lagoon complexes (secondary wastewater treatment facilities; hereafter, lagoons). On average, lagoon complexes were composed of three individual lagoons or "cells" (range = 1–7), but not all cells supported nesting Red-winged Blackbirds. We sampled 10, 14, and 19 ponds in 1999, 2000, and 2001, respectively. Cattails (*Typha* spp.) dominated the emergent vegetation at both ponds and lagoons, but, relative to ponds, lagoons had only a thin strip of cattails around their perimeters. Most lagoon complexes were bordered by agricultural crops and old-fields, but mixed deciduous forests partially bordered several lagoons. Ponds were bordered mainly by old-fields and mixed deciduous forests.

Time of ice breakup during early spring was similar on lagoons and ponds, with the exception of one aerated lagoon cell that became ice-free earlier. During the study period, water levels in ponds did not fluctuate >1 m, either seasonally or annually. In contrast, average water depth within and among sewage lagoon complexes varied seasonally between 2 and 5 m, but large fluctuations in water depth usually occurred outside of the Red-

winged Blackbird's breeding season. In 2000, water levels at 7 of 10 lagoon sites were lowered in mid-May; thus, only the remaining three lagoons were sampled.

Despite obvious physical differences between lagoons and ponds, Zimmerling (2002) showed that populations of female Red-winged Blackbirds in the eastern Ontario study area were demographically (juvenile: adult) similar and that morphological characteristics (i.e., culmen, wing chord, tarsus length, and body mass) of females also did not differ between habitats. In addition, although lagoons and ponds differed marginally in shape and size, the maximum number of active nests/1,000 m<sup>2</sup> of wetland (based on measurements of wetland perimeters) were similar between habitats (Zimmerling 2002). In contrast, the maximum number of active nests/1,000 m<sup>2</sup> of emergent vegetation (*Typha* spp.) within wetlands was four times higher at lagoons than at ponds (8.4 versus 2.1) because suitable nesting habitat (i.e., emergent vegetation) was restricted.

**Field methods.**—Nests were discovered during twice-weekly searches of emergent vegetation. Nests were marked with flagging tape and monitored daily. Using remote temperature sensors (Hobo Temp XT, Onset Computer Co., Pocasset, Massachusetts), we assessed incubation patterns of female Red-winged Blackbirds at 406 nests (1999, 2000, and 2001,  $n = 59/45$  [lagoon/pond], 38/69, and 115/80, respectively). After the second egg of a clutch was laid, but before the third egg was laid, a thermistor attached to a Hobo Temp data logger was slowly worked into the nest from underneath until it was <5 mm above the nest lining. The thermistor was set <5 mm above the nest lining to prevent contact with the incubating female's brood patch. Thermistors set higher than this level were usually discovered and physically removed by the female, and, on six occasions, the nest was abandoned. To minimize detection by incubating females and predators, data loggers were wrapped in plastic and concealed in vegetation 2 to 6 m from the nest.

Data loggers continuously recorded temperature variations at 2.5-min intervals for up to 13 consecutive days, which spanned the entire incubation period (a 2.5-min sampling interval was the shortest possible interval that

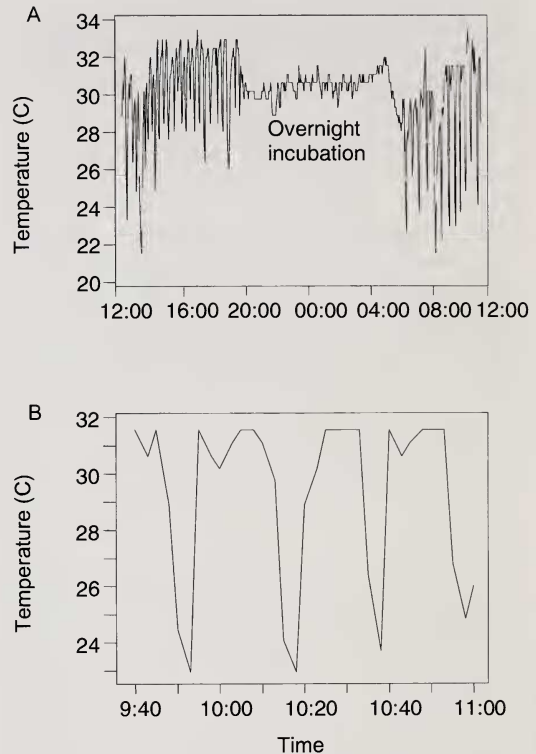


FIG. 1. (A) Temperature recorded at a single Red-winged Blackbird nest at a lagoon in Perth, Ontario over a 24-hr period, 2–3 June 2001. The overnight incubation session lasted from 19:53 to 06:53 EST. (B) An expanded 90-min section of this trace shows high nest temperature when the parent is incubating and sharply falling temperature during daytime foraging bouts when the nest is left unattended. Arrivals and departures of the incubating adult result in sudden, obvious changes in nest temperature.

could be maintained for 13 days without overloading the logger's memory capacity). After hatching was complete (i.e., when 2 days had elapsed since the last egg hatched), data loggers and thermistors were removed from nests.

Incubation patterns were extracted after downloading data from loggers using Boxcar Pro 4.0 software (Onset Computer Co., Pocasset, Massachusetts). Because thermistors did not contact the female's brood patch, but instead, recorded air temperature at the bottom of the nest bowl, recorded temperatures were lower than the 34–39°C temperatures required for optimal embryo development (Fig. 1). Nonetheless, periods when a female was incubating versus absent from the nest showed

as clear peaks and troughs on the temperature traces, allowing times of arrival and departure to be estimated. We acknowledge that data regarding time periods are estimates due to factors such as lags in temperature changes and data loggers recording temperature every 2.5 min rather than continuously; however, combining a large number of readings ( $n = 6,300\text{--}7,400$ ) over the course of the incubation period, and considering that these factors should have affected birds similarly in pond and lagoon habitats, their effects should have been minimal. To verify that arrival and departure times were accurately discerned from temperature traces, we positioned video cameras (Sony 8 mm Handycams) 10 m from a subset of nests ( $n = 6$ ) and video-recorded female incubation patterns for 1 hr (6 hr total). Comparisons of video recordings and temperature traces ( $n = 144$  data points) indicated that departure and arrival times at the nest were accurately identified from the temperature traces. On the basis of these observations, we interpreted any drop in temperature of more than  $4^{\circ}\text{C}$  that occurred within a 5-min period as a departure from the nest (i.e., the start of a foraging bout). Any similar rise in temperature signified an arrival at the nest (initiating a bout of attentiveness). Hence, during the daytime (06:00–20:00 EST), duration of foraging bout was calculated as the number of minutes between two successive bouts of attentiveness. Duration of attentiveness bout was calculated as the number of minutes between two successive foraging bouts. Because duration of attentiveness and foraging bouts may be influenced by number of foraging bouts, we calculated the number of foraging bouts/hr as the number of foraging bouts/total hr of daylight. We also calculated incubation constancy (percentage of daytime spent incubating) as total duration of attentiveness bout / (total duration of attentiveness bout + total duration of foraging bout) to evaluate whether differences, if any, in duration of attentiveness or foraging bouts and/or number of foraging bouts/hr influenced incubation constancy. Because variation in the duration of overnight incubation could indicate differential use of endogenous reserves, we calculated overnight incubation as the number of minutes between returning to the nest for the last time in the evening and leaving the nest the first time in

the morning. Females never left the nest during the night.

Temperature traces for nests with data loggers confirmed that onset of incubation in Red-winged Blackbirds occurs with the laying of the penultimate egg (e.g., Yasukawa and Searcy 1995). For nests without data loggers, incubation onset was assumed to have occurred once the penultimate egg was laid, but was also confirmed by temperature of the clutch. Nine days after incubation onset, nests with and without data loggers were checked daily to determine hatch date. Because Red-winged Blackbird clutches sometimes hatch asynchronously (Yasukawa and Searcy 1995), nests were visited at least once daily during hatching to record the sequence of hatching and to determine length of the incubation period (calculated as the time between laying of the penultimate egg and when the majority of eggs had hatched). However, in 1999, some nests were monitored only every other day, in which case nestling age ( $\pm 6$  hr) was estimated based on nestling size and wetness of their natal down (Zimmerling 2002). After hatching was complete, hatchability (i.e., number of eggs hatched/total number of eggs laid) was recorded.

Between 3 and 18 June 2001, we quantified foraging behavior for a subset of incubating females ( $n_{\text{lagoon}} = 7$  and  $n_{\text{pond}} = 5$ ) at two sewage lagoons (one bordered by agricultural fields and one partially bordered by uplands) and three beaver ponds. Most birds in the study area were not color-banded, but we identified individual females by following them away from their nests when observing them during foraging bouts. Foraging observations were conducted between 07:00 and 12:00 and began when the female left the nest and ended when the female returned to the nest (one data point per individual). For each female, we recorded the habitat(s) in which she foraged (i.e., emergent vegetation, shoreline, or forest-edge) and mean distance of foraging habitat(s) from the nest.

*Statistical analyses.*—We obtained relatively few temperature traces that covered the entire incubation period of a nest ( $n_{\text{lagoon}} = 19$ ,  $n_{\text{pond}} = 15$ ). For statistical analysis, we included all temperature traces with a minimum of 8 days of continuous recording during incubation ( $n_{\text{lagoon}} = 43$ ,  $n_{\text{pond}} = 39$ ) to increase

total sample size ( $n_{\text{lagoon}} = 62$ ,  $n_{\text{pond}} = 54$ ). Incomplete temperature traces were usually the result of nest predation or the female removing the thermistor during incubation; these were excluded from the analysis. We calculated mean incubation constancy (%), mean number of foraging bouts/hr, mean bout duration of attentiveness (min) and foraging (min), and mean overnight incubation (min) for all temperature traces with  $\geq 8$  days of continuous recording. For analysis of incubation period and hatchability, we combined datasets from nests with and without data loggers ( $n_{\text{lagoon}} = 138$ ,  $n_{\text{pond}} = 107$ ). To analyze hatchability, all eggs lost at active nests by causes other than hatching failure (i.e., predation, drowning, nest collapse, or clutch desertion) were excluded.

We used an information-theoretic approach for model selection (Burnham and Anderson 1998). We considered several *a priori* candidate models for each response variable that included main effects and a subset of interactions that were of interest. Model selection was done using Akaike's Information Criterion (AIC) with corrections for small sample size ( $AIC_c$ ) using PROC MIXED (SAS Institute, Inc. 2001) with the IC option for model estimation. Models were ranked using  $\Delta AIC_c$  (Burnham and Anderson 1998) and were calculated as  $\Delta AIC_c = AIC_{ci} - AIC_{cmin}$  where  $\Delta AIC_{ci}$  was the  $i^{\text{th}}$  model from a candidate set. Akaike weights ( $w_i$ ) were calculated to assess the relative likelihood of each model being the best model.

Because we were interested in the effects of habitat-related differences in incubation patterns of female Red-winged Blackbirds, all candidate models included effects of habitat (lagoon versus pond) as an explanatory variable. Because incubation patterns in some species may vary temporally (e.g., Conway and Martin 2000b), year (coded 1, 2, 3 for 1999, 2000, and 2001, respectively) and nest-initiation date (date first egg was laid; May 1 = 1) were also used to generate a set of candidate models. Model selection was done separately for incubation period, incubation constancy, duration of foraging bout, foraging bouts/hr, duration of attentiveness bout, duration of overnight incubation, and hatchability, respectively. The set of candidate models was the same for each dependent variable and includ-

ed effect of habitat (HAB), nest-initiation date (ID), year (YR), and all two-way interactions involving habitat. A null model (intercept only) was also included as a candidate model. Only candidate models with  $\Delta AIC_c < 2.0$  are presented. When no candidate models had  $\Delta AIC_c < 2.0$ , second-best models are presented.

## RESULTS

*Incubation period.*—The best model explained 14% of variation in incubation period and included habitat (HAB), year (YR), and habitat-by-year interaction ( $HAB \times YR$ ) as predictors (Table 1). Likelihood of model fit for {HAB, YR,  $HAB \times YR$ } was  $>9\times$  that of the second-best model ({HAB, YR, ID,  $HAB \times YR$ },  $\Delta AIC_c = 4.4$ ). Incubation period was longer at ponds than at lagoons, but this difference varied with year. In 1999, incubation period was 0.8 days longer at ponds than at lagoons, but was only 0.2 days longer in each of the following 2 years.

*Incubation constancy.*—The model {HAB} was superior to other models considered, and explained 9% of variation in incubation constancy (Table 1). Likelihood of model fit for {HAB} was  $>5\times$  that of the second-best model ({HAB, YR,  $HAB \times YR$ },  $\Delta AIC_c = 3.5$ ). Incubation constancy was 4% lower at ponds than at lagoons (69% versus 73%) and this difference did not vary with nest-initiation date or year.

*Duration of foraging bout.*—The best model explained 12% of variation in duration of foraging bout and included habitat (HAB), initiation date (ID), and habitat-by-initiation date ( $HAB \times ID$ ) interaction as predictors (Table 1). Likelihood of model fit for {HAB, ID,  $HAB \times ID$ } was  $>4\times$  that of the second-best model ({HAB, ID},  $\Delta AIC_c = 3.2$ ). Duration of foraging bout averaged longer at ponds (8.9 min) than at lagoons (8.1 min) and the difference increased with nest-initiation date.

*Foraging bouts/hr.*—We found considerable model-selection uncertainty for foraging bouts/hr and no predictors appeared particularly important (Table 1). Moreover, the null model, which contained no predictors, had the lowest  $AIC_c$  score of any models. Even the most complex model {HAB, ID, YR,  $HAB \times ID$ ,  $HAB \times YR$ } explained only 3% of variation in foraging bouts/hr.

TABLE 1. Model selection for variation in incubation period<sup>a</sup> (days), incubation constancy (%), duration of foraging bout (min), foraging bouts/hr, duration of attentiveness bout (min), duration of overnight incubation (min), and hatchability<sup>a,b</sup> of female Red-winged Blackbirds nesting at lagoons ( $n = 62$ ) and at ponds ( $n = 54$ ) in eastern Ontario, in relation to habitat (HAB, pond versus lagoon), nest-initiation date (ID, May 1 = 1), and year (YR, 1999–2001). Shown for each model are numbers of parameters (K), AIC difference with correction for small sample sizes ( $\Delta AIC_c$ ), model weight ( $w_i$ ), proportion of variance explained ( $R^2$ ), and Least Square Means  $\pm$  SE.

Response variable	Model	K	$\Delta AIC_c$	$w_i$	$R^2$	Ponds	Lagoons
Incubation period	HAB, YR, HAB $\times$ YR	7	0.0	0.896	0.14	12.4 $\pm$ 0.1	12.0 $\pm$ 0.1
	1999					12.7 $\pm$ 0.1	11.9 $\pm$ 0.1
	2000					12.6 $\pm$ 0.1	12.4 $\pm$ 0.1
	2001					12.1 $\pm$ 0.1	11.9 $\pm$ 0.1
	HAB, YR, ID, HAB $\times$ YR	8	4.4	0.099	0.15	12.4 $\pm$ 0.1	12.0 $\pm$ 0.1
Incubation constancy	HAB	3	0.0	0.851	0.09	69.3 $\pm$ 0.1	73.4 $\pm$ 0.1
	HAB, YR, HAB $\times$ YR	7	3.5	0.147	0.09	69.3 $\pm$ 0.1	73.1 $\pm$ 0.1
Duration of foraging bout	HAB, ID, HAB $\times$ ID	5	0.0	0.801	0.12	8.9 $\pm$ 0.2	8.1 $\pm$ 0.2
	HAB, ID	4	3.2	0.171	0.06	8.6 $\pm$ 0.2	8.0 $\pm$ 0.2
Foraging bouts/hr	NULL	2	0.0	0.689	0.00		
	HAB	3	1.8	0.280	0.01	2.2 $\pm$ 0.1	2.1 $\pm$ 0.1
Duration of attentiveness bout	HAB, ID	4	0.0	0.638	0.06	30.6 $\pm$ 1.6	32.2 $\pm$ 1.5
	HAB, ID, HAB $\times$ ID	5	1.4	0.316	0.06	30.6 $\pm$ 1.5	32.1 $\pm$ 1.5
Duration of overnight incubation	NULL	2	0.0	0.883	0.00		
	HAB	3	3.2	0.059	0.01	537.5 $\pm$ 11.5	545.1 $\pm$ 12.8
	HAB	3	4.8	0.083	0.01	87.8 $\pm$ 0.1	85.6 $\pm$ 0.1

<sup>a</sup> Number of nests in model = 361 (161 pond, 200 lagoon).

<sup>b</sup> Total number of eggs = 1,353 (581 pond, 772 lagoon).

*Duration of attentiveness bout.*—The model {HAB, ID} was superior to other models considered and explained 6% of variation in duration of attentiveness bout (Table 1). Likelihood of model fit for {HAB, ID} was 2 $\times$  that of the second-best model ({HAB, ID, HAB  $\times$  ID},  $\Delta AIC_c = 1.4$ ), which also contained nest-initiation date as a predictor. Duration of attentiveness bout was 1.6 min shorter at ponds than at lagoons. Regardless of habitat, the duration of attentiveness bout increased by 0.3 min for each later day of nest initiation.

*Duration of overnight incubation.*—There was considerable model-selection uncertainty for duration of overnight incubation and no predictors appeared particularly important (Table 1). Moreover, the null model, which contained no predictors, had the lowest  $AIC_c$  score of any models considered. Even the most complex model {HAB, ID, YR, HAB  $\times$  ID, HAB  $\times$  YR} explained only 2% of variation in duration of overnight incubation.

*Hatchability.*—Model selection for variation in egg hatchability was equivocal and no predictors in the set of candidate models appeared important (Table 1). Moreover, the null model, which contained no predictors, had the lowest  $AIC_c$  score of any models considered. Furthermore, among the set of candidate models, the most complex model {HAB, ID, YR, HAB  $\times$  ID, HAB  $\times$  YR} explained only 3% of the variation in hatchability.

*Foraging behavior.*—Incubating females nesting at ponds foraged >2 $\times$  farther away from their nests than did females nesting at lagoons (94  $\pm$  38 m versus 46  $\pm$  23 m). At ponds, all five females foraged within forest edges, although one female was observed capturing a flying insect (Odonata) over emergent vegetation. At lagoons, incubating females always foraged within the emergent vegetation, but on three occasions, they also foraged along lagoon shorelines.

## DISCUSSION

Many studies have demonstrated that insect abundance is greater (or insects are more easily acquired) at sewage lagoons than in other habitats (e.g., Swanson 1977, Piest and Sowls 1985, Porter 1993, Zimmerling 2002). Quinney (1983) showed that insect biomass at a sewage lagoon in southwestern Ontario was approximately 10 times greater than that at a nearby field habitat during the period when most Tree Swallows were incubating eggs. Many of these same studies also have revealed that the type of insects available to birds at sewage lagoons is different from that available in other habitats (e.g., Swanson 1977, Quinney 1983, Zimmerling 2002). During brood-rearing, Zimmerling (2002) found that female Red-winged Blackbirds at sewage lagoons in eastern Ontario usually foraged close to their nests and captured numerous flying insects (Family Chironomidae), whereas females at beaver ponds generally foraged much farther from their nests, often in adjacent uplands, and usually returned to the nest with one and sometimes two large insects, often from the Family Noctuidae (Zimmerling 2002). Thus, presuming that insect availability and/or the type of insects available at lagoons and ponds were different, we could examine the response of Red-winged Blackbird incubation patterns, incubation period, and hatchability of eggs to habitat-related differences in foraging behavior.

Incubation periods of Red-winged Blackbirds at lagoons were shorter than those at ponds. Other investigators (see references in Martin 1987, Williams 1996, Hebert 2002) have suggested that shorter incubation periods are a consequence of increased attentiveness during incubation. At lagoons, incubation constancy was 4% higher than it was at ponds, but because substantial variation in Red-winged Blackbird incubation constancy (range = 65–72%) has been reported elsewhere (e.g., Holcomb 1974), these results should be interpreted cautiously. Nonetheless, our results suggest that lower nest attentiveness at ponds compared with that at lagoons could be explained by habitat-related differences in foraging behavior, resulting in longer duration of foraging bouts and shorter duration of attentiveness bouts without changing the frequency

of foraging bouts. For example, although our behavioral observations were limited, female blackbirds incubating at ponds—unlike females at lagoons—did not forage within the emergent vegetation in close proximity to the nest; rather, they foraged much farther from the nest along forest-edges of woodlots bordering the ponds. Our behavioral observations of female foraging habits at ponds were similar to those found in other studies: marsh-nesting female Red-winged Blackbirds spend much of their time foraging in uplands that border their nesting habitat (e.g., Orians 1980, 1985; Whittingham and Robertson 1994; Turner and McCarty 1998) because of limited food availability within the marsh. It seems unlikely that food availability was limited within sewage lagoons in our study area because, even at the lagoon bordered by upland habitat, females were observed foraging only in the emergent vegetation and/or along the shoreline.

Although it was not possible to taxonomically categorize insects taken by foraging females during incubation, other studies in eastern Ontario have revealed that, during the brood-rearing period, females that foraged in upland habitats consistently delivered lepidopteran larvae to their broods (Bendell and Weatherhead 1982, Zimmerling 2002). Less than 65 km from our study area, Bendell and Weatherhead (1982) showed that female Red-winged Blackbirds fed lepidopteran larvae of the family Noctuidae (55% by volume) to their nestlings, of which larvae of a single species, *Amphipoea velata* (Walker), made up 31% of the total volume. In contrast, female passerines nesting at sewage lagoons feed nestlings chironomid adults (Quinney 1983, Zimmerling 2002), the most abundant insect at lagoons (Swanson 1977, Hussell and Quinney 1987). It is possible that female Red-winged Blackbirds incubating at ponds were searching for lepidopteran larvae in the upland habitats during foraging bouts, and, because many lepidopterans are cryptically colored, additional search time may have been required for females to find these insects. Therefore, female Red-winged Blackbirds foraging in upland habitats in eastern Ontario may have incurred costs associated with increased travel time and energy expenditure for food gathering, which may have resulted in longer for-

aging bouts, shorter bouts of attentiveness, and, ultimately, longer incubation periods.

We found annual variation in incubation patterns and incubation period, which may have been attributable to annual environmental variability. We are aware of only two studies of passerines that assessed annual variation in food supply and incubation patterns (Drent et al. 1985, Moreno 1989). Moreno (1989) found that, during the coldest year of his study, incubation length was negatively correlated with the amount of supplemented food he provided to incubating female Northern Wheatears. Similarly, Drent et al. (1985) found that when European Starlings' (*Sturnus vulgaris*) principle prey, crane fly larvae (*Tipula paludosa*), were scarce, incubating females responded by decreasing incubation constancy and increasing the length of foraging bouts. Relatively warm spring temperatures in 1999 in eastern Ontario may, in part, explain the nearly 1-day difference in incubation period between lagoons and ponds in 1999 compared with 2000 and 2001. Mean monthly temperature for May 1999 was 16.5° C, which was 3° and 2° C warmer than in 2000 and 2001, respectively. It is unlikely that annual variation in incubation period and differences observed between lagoons and ponds were the direct result of ambient temperature because both habitat types were sampled throughout eastern Ontario. Instead, differences in incubation period may have been due to habitat-related differences in type and/or abundance of insects available to incubating females. For example, the largest emergence of chironomids at two lagoon sites in eastern Ontario occurred 6 and 4 days earlier in 1999 than in 2000 and 2001, respectively (JRZ pers. obs.). Regardless, we did not assess dietary habits of incubating females (neither were they assessed in other studies of Red-winged Blackbirds); thus, we cannot preclude the possibility that other factors were responsible for annual variation in incubation period within and between habitats.

The importance of habitat and food availability in affecting seasonal variation in passerine incubation patterns is equivocal because nest attentiveness is positively correlated with ambient temperature in north-temperate environments (Zerba and Morton 1983, Conway and Martin 2000a). Conway and

Martin (2000a) proposed that the metabolic energy required by small birds during incubation decreases with increased ambient temperature and should allow individuals to increase length of attentiveness bouts because they are metabolizing energy reserves more slowly. In our study, duration of attentiveness bout increased with nest-initiation date, which was a proxy for increasing ambient temperatures during spring and summer. Food availability also may have increased (whether directly or indirectly) with ambient temperature during May, when the majority of females were incubating (also see Quinney 1983). Thus, increased rates of food acquisition (in response to increased food availability) may explain the decline in duration of foraging bout with nest-initiation date in both habitats. Not surprisingly, because of inherent difficulties in separating the effects of ambient temperature and food availability, few passerine studies, including ours, have unambiguously demonstrated a relationship between seasonal changes in incubation patterns and food availability.

It is possible that incubation patterns of female Red-winged Blackbirds did not differ between wetland habitats due to differential female foraging habits, but, rather, to differences in female age, female body size, nest predation, or the use of endogenous reserves. However, Red-winged Blackbird populations at lagoons and ponds in our study area were similar with respect to female age structure, body mass, and structural size (Zimmerling 2002). Moreover, Wheelwright and Beagley (2005) suggested that incubation behavior in Savannah Sparrows (*Passerculus sandwichensis*) is largely innate and unaffected by prior reproductive experience or other age-related variables. Other studies have suggested that predation risk can be an important factor influencing incubation behavior in some passerines (e.g., Ghalambor and Martin 2002, Martin 2002). However, in eastern Ontario, the proportion of Red-winged Blackbird nests depredated during incubation at beaver ponds, sewage lagoons, and roadside ditches (which resemble lagoons in vegetation structure) was similar, despite differences in primary predators (i.e., avian versus mammalian) in each habitat (JRZ unpubl. data). Although little is known about use of endogenous reserves by



incubating passerines, most studies indicate that passerines use exogenous nutrients for incubation (see Williams 1996, Conway and Martin 2000b). Some studies have shown mass loss by incubating females, but that may have been due to post-laying atrophy of reproductive organs rather than to loss of somatic tissue (Ricklefs and Hussell 1984). Moreover, overnight incubation represents a prolonged period of fasting coinciding with minimum daily ambient temperatures; therefore, if endogenous reserves were used more heavily by Red-winged Blackbirds at lagoons than at ponds, then duration of overnight incubation should have been longer at lagoons, but it was not. To better assess whether endogenous reserves were used differentially during incubation by female Red-winged Blackbirds nesting at lagoons, researchers should compare levels of endogenous reserves between onset and termination of overnight incubation.

In some species, shorter incubation periods and bouts of attentiveness can improve hatching success, which is influenced by temperature of eggs during incubation (Lyon and Montgomerie 1985, Nilsson and Smith 1988, Strausberger 1998; but see Eikenaar et al. 2003). We did not, however, detect a difference in hatchability of Red-winged Blackbird eggs between lagoons and ponds (85.6% versus 87.8%). Unlike some passerines that nest in the high arctic and take long foraging bouts (i.e., 20 min; Lyon and Montgomerie 1985, 1987), female Red-winged Blackbirds nesting at both lagoons and ponds generally took short foraging bouts (i.e., <10 min; also see Holcomb 1974), perhaps explaining the similarity in egg hatchability between habitat types. In other studies of Red-winged Blackbirds, egg hatchability ranged from 87.9% (Williams 1940) to 97.0% (Young 1963). It is possible that when egg size measurements were taken (for another study), some of the eggs in this study were damaged (dimpled or hairline cracked) by calipers, thus accounting for the relatively low hatchability of Red-winged Blackbird eggs in both habitats.

Comparisons of Red-winged Blackbirds nesting in two different habitats—sewage lagoons and beaver ponds—in eastern Ontario suggested that differences in incubation periods, incubation constancy, and bout duration

of attentiveness and foraging may have been responses to differential foraging habits, possibly as a result of differences in food acquisition during incubation. Differences in foraging habits, however, did not affect hatchability. Until further research and experimental work is extended to many other species, it will be difficult to judge the importance of variation in foraging habits and/or food acquisition in influencing incubation patterns and hatchability in passerines.

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